New Decapoda (Anomura, Brachyura) from the Eocene Bateque and Tepetate Formations, Baja California Sur, México

Carrie E. Schweitzer[1], Rodney M. Feldmann[2], Gerardo González-Barba[3], and Vlasta Ćosović[4]

[1]Department of Geology, Kent State University Stark Campus, 6000 Frank Ave. NW, North Canton, Ohio 44720 USA
<cschweit@kent.edu>
[2]Department of Geology, Kent State University, Kent, Ohio 44242 USA <rfeldman@kent.edu>
[3]Departamenta de Geologia, UABCS, C.P.23080, La Paz, Baja California Sur, Mexico <gerardo@uabcs.mx>
[4]Department of Geology and Paleontology, Faculty of Science, University of Zagreb, Croatia <vlasta1501@yahoo.com>

Abstract

Unusually preserved decapod specimens from the Eocene Bateque Formation of Baja California Sur, México, have heretofore been undescribed. This robust fauna has yielded thirteen taxa with seven new species, including *Homola bajaensis*, *Raninoides acanthocolus*, *R. proracanthus*, *Prehepatus mexicanus*, *Daldorfia salina*, *Anatolikos undecimspinosus*, and *Paracorallicarcinus tricarinatus*. In addition, several taxa are identifiable to the family level. *Laeviranina* is synonymized with *Raninoides*, resulting in numerous new combinations. The Bateque Formation fauna has yielded the oldest known occurrence of *Anatolikos*, *Homola*, *Daldorfia*, and the Daldorfiidae as well as the first notice of *Prehepatus* in the Eocene and the first articles of the cheliped of *Prehepatus* other than those of the chelae. Micropaleontological interpretation of the sediments collected at Pelican Island suggests that the Bateque Formation at that location was deposited in an oligotrophic, outer shelf or platformal setting, in water of at least 30 m depth. The decapods of the Bateque Formation exhibit Tethyan and North Pacific distributional patterns and are a mixture of warm and cool, shallow, epicontinental, and deep water taxa. These patterns are interpreted to be a result of Baja California's Eocene position in the crossroads of the North Pacific and Tethyan distributional pathways.

Key words: Decapoda, Brachyura, Anomura, Eocene, Bateque Formation, Baja California, Mexico

Introduction

Since the groundbreaking work of Rathbun (1930b), the number of fossil decapod crustaceans known from Baja California has increased in recent years (Schweitzer *et al*., 2002; 2006 [imprint 2005]; Schweitzer, 2005). Baja California is a key area in understanding the evolution of these animals, because during the Eocene, it was positioned within two major dispersal pathways, the North Polar and the Tethyan (Schweitzer, 2001b; Schweitzer *et al*., 2002).

Geologic Setting

Bateque Formation

Geology: Schweitzer *et al*. (2006 [imprint 2005]) recently summarized the geology of the Bateque Formation. There have been discrepancies in determining the age of the Bateque Formation, which primarily appear to be based upon the area of outcrop. The formation in the northernmost part of the outcrop area, in the vicinity of Laguna San Ignacio and Mesa La Salina (Fig. 1), has been correlated with the "Capay Stage" in California

of Givens (1974), considered to be of middle early Eocene age (Squires, 2001, and references therein), according to Squires and Demetrion (1990a, 1994a) and Squires (2001). Our analysis of the foraminifers preserved at localities at Pelican Island in Laguna San Ignacio indicates an age of middle to upper Eocene. McLean *et al*. (1985, 1987) and McLean and Barron (1988) described late middle Eocene diatoms of zones CP14a and CP14b from some of the southernmost outcrop areas of the Bateque Formation. Later workers have concurred with the middle Eocene age for this area (Squires and Demetrion, 1990b; Sandy *et al*., 1995).

The invertebrate paleontology of the northern outcrops of the Bateque Formation has been well-studied. Red algae, foraminifers, sponges, solitary corals, bryozoans, polychaetes, bivalves, gastropods, nautiloids, crabs, and sea urchins have all been described from these outcrops (Squires and Demetrion, 1989; 1990a, b, c; 1992; 1994a, b; 1995; Squires and Saul, 1997; Schweitzer *et al*., 2006 [imprint 2005]). The decapods from the Bateque Formation described here were collected from northern localities, near San Ignacio town.

Micropaleontological description of Bateque Formation at Pelican Island: Lithologic specimens for micropaleontological
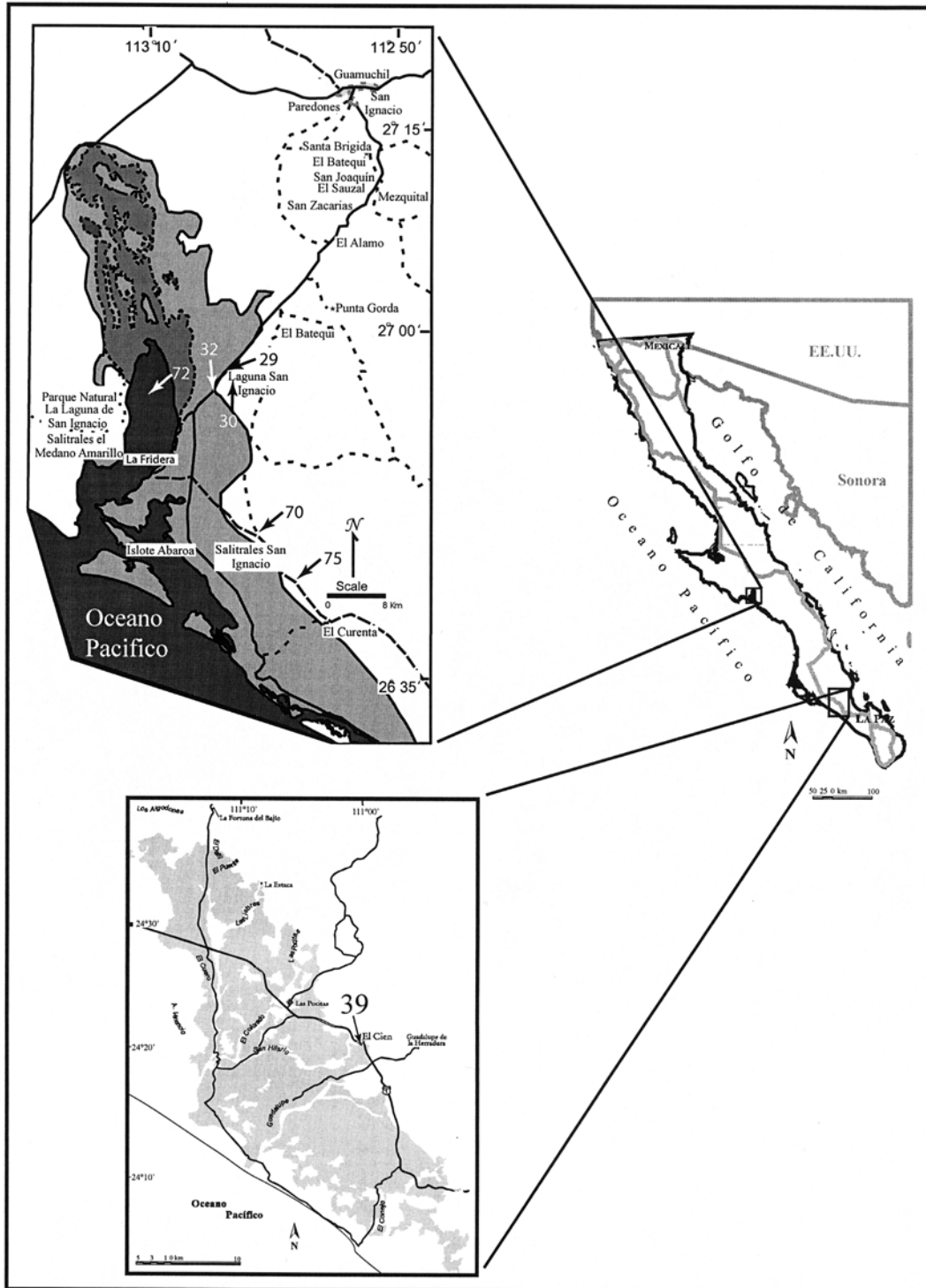
Fig. 1. Locality maps, showing locations where specimens were collected. Magnified area at upper left is Bateque Formation area of outcrop; magnified area at lower left is Tepetate Formation area of outcrop. Arrows and numbers denote Waypoint locations referred to in text.

examination were collected from Pelican Island in Laguna San Ignacio (Waypoint 72); localities on that island yielded numerous macrofossils including gastropods, annelid worm tubes, echinoids, and bryozoans, but only one decapod chela, probably a callianassid ghost shrimp (MHN-UABCS/Ba8-1). The well-sorted sandstone is defined by well-preserved, unbroken, rotaliid foraminifera including flat, large *Proporocyclina tobleri* (Vaughan and Cole,

1941), which are 4 mm in diameter and comprise 5–20% of the total clasts (estimation based on charts from Flugel, 2004, p. 258). Other clasts include robust (thickness to diameter ratios of 1) and flatter (T/D ratio of 0.5) amphisteginids, such as *Amphistegina pregrimsdalei* Caudri, 1974, together comprising up to 20% of the total clasts, and rare nummulitids (*Heterostegina* sp.?), comprising 0–5% of the total clasts. Sporadically miliolids and smaller

benthic foraminifera such as *Gyroidinoides* sp. are found. Microfacies are also characterized by the presence of branching bryozoan colonies (1–10%), crinoid plates (0–5%), and broken and encrusted bivalve fragments (0–5%) and serpulinids. Encrustations are composed of red algae and are developed on both sides of larger bivalve fragments. Most of the robust amphisteginid and some of the proporocyclinidal tests are slightly micritized, indicating a long residence time of the tests on the sea-bottom.

Paleoecological interpretation of Bateque Formation at Pelican Island: The restricted larger benthic foraminiferal assemblage, the occasional occurrence of porcellaneous foraminifers, and the dominance of flat and large proporocyclinids suggest an outer platform or shelf setting within the photic zone. Increasing size and degree of flatness of orbitoidal foraminifera can be interpreted to reflect increasing water depth (Hallock and Glenn, 1986; Hottinger, 1997, Ćosović *et al.*, 2004), but within the photic zone. Robust morphologies of amphisteginids are most common in shallow, high-energy environments, generally in less than 30 m of water depth (Hallock and Hansen, 1979). Flatter morphologies are typical of deeper water, lower light and energy conditions, below 60 m (Hallock, 1999) and from 80 to 140 m (Reiss and Hottinger, 1984). Modern amphisteginids live on both firm and soft substrates. The presence of robust, well preserved amphisteginids (micritization of the tests occurred in shallow-water environs) implies that their tests were transported along with bivalves and miliolids into a deeper-water setting by debris flows or periodic storm action.

The analyzed sediment was deposited under oligotrophic conditions, suggested by the presence of symbiont-bearing benthic foraminifera, in an outer platformal or outer shelf setting, indicated by the dominance of flat, orbitoidal specimens and the general absence of planktonic and porcellaneous foraminifera at a water depth greater than 30 m, with the maximum possible depth being the lowermost limit of the photic zone.

Tepetate Formation

Geology: The geology of the Tepetate Formation has been recently summarized (Schweitzer *et al.*, 2002; 2006 [imprint 2005]). Macrofossils known from the unit include pelecypods, gastropods, echinoids, decapod crustaceans, shark teeth, and birds (Rathbun, 1930b; Squires and Demetrion, 1990c; 1992; Perrilliat, 1996; González-Barba, 2000, 2003; González-Barba and Thies, 2000; González-Barba *et al.*, 2002; Schweitzer *et al.*, 2002); the macrofaunal assemblage is apparently much less robust in the Tepetate than in the Bateque Formation. Although some workers have considered the Tepetate Formation to be very similar to the Bateque Formation (Squires and Demetrion, 1991; 1994a), or even synonymous (Hausback, 1984), we consider that the two formations are separate, based upon their differing lithologies and contained macrofossils. There are very few shared species between the two units, including some shark and ray species and few decapods (Table 1).

Occurrence and Preservation

The occurrence and preservation of the decapod specimens forming the basis for this study is highly unusual. Decapod specimens were collected from the enclosing rocks, composed of weakly cemented fine sandstone, by breaking the rocks into small pieces. The decapods were neither found on particularly fossiliferous bedding planes nor in concretionary structures. The sandstone lacked discernable bedding structures. Rather, the decapods were enclosed within the rocks, exhibiting no particular orientation. Specimens were not visible on the surface of the rocks; hence, there was no way of knowing the decapods would be found in the rocks. Had it not been for the chance smashing of rocks by one of our graduate students, the specimens would have gone unnoticed.

Decapod crustacean occurrences typically are in concretions or are otherwise visible at the surface due to the different color of the cuticle compared to sediments and other fossils. Often, specimens are concentrated on specific bedding planes which also enhances the probability of discovery. Those specimens that may have been exposed at the surface in the Bateque Formation described herein are sufficiently fragile and the enclosing sandstone is so friable that the fossils would be made unrecognizable almost immediately upon exposure at the surface by weathering processes. The delicate nature of the specimens coupled with their small size made discovery quite serendipitous.

Preservation of the specimens is also unusual. Because most of the specimens were collected very near to sea level, the highly permeable rocks were often saturated by saltwater and the high evaporation rate in the region resulted in concentration of salts on, or near, the surface. As a result, the specimens within the rock were heavily infused with salt (they taste salty). Any cementing agent that bound the sandstone together has been removed so that the rock is now cemented solely by salt. This makes cleaning the specimens with any type of aqueous solution potentially disastrous, as detail can literally dissolve away.

Several attempts were made to clean the specimens, none of which was particularly successful. When the specimens were initially cleaned with dental instruments and with airscribes, the matrix smeared out in a manner similar to putty. Attempting to carefully disaggregate the sediment using various liquids was also unsuccessful. Alcohol and acetone had no effect on the matrix. Immersion of trial specimens in distilled water resulted in the complete disaggregation of the sediment and concomitant destruction of the specimen. More careful application of water, for example, by placing the specimen in a pan of water with only the base of the rock immersed, also resulted in the destruction of the specimen. Water moved up through the specimen by capillary action, as was intended; however, as the salt dissolved, the cuticle that was present on the specimen curled away from the rock and was lost. As a result of these efforts, it was concluded that very little could be done to clean and prepare the specimens in the

Table 1. Decapod species known from the Eocene Bateque and Tepetate formations. Presence of the species is indicated with a number "1" in the appropriate column. Higher level taxonomy is given for informational purposes. *Rathbun (1930b) reported *Montezumella tubulata* from Arroyo Colorado in Lower California but did not give a formation name; Mina-Uhink (1957) considered that locality to be the type section for the Tepetate Formation. Thus, we consider it to be from the Tepetate Formation.

Taxon	Bateque	Tepetate
Infraorder Thalassinidea Latreille, 1831		
Superfamily Callianassoidea Dana, 1852		
Family Callianassidae Dana, 1852		
Subfamily Callichirinae Manning and Felder, 1991		
Neocallichirus cf. *N. rhinos* Schweitzer and Feldmann, 2002	1	
Neocallichirus sp. *in* Schweitzer *et al.*, 2006 [imprint 2005]	1	
Callianassidae *sensu lato* species 1 *in* Schweitzer *et al.*, 2006[imprint 2005]	1	
Callianassidae *sensu lato* species 2 *in* Schweitzer *et al.*, 2006 [imprint 2005]	1	
Callianassidae *sensu lato* species 3 *in* Schweitzer *et al.*, 2006 [imprint 2005]	1	
Callianassidae *sensu lato* species 4 *in* Schweitzer *et al.*, 2006 [imprint 2005]	1	
Callianassidae *sensu lato* species 5 *in* Schweitzer *et al.*, 2006 [imprint 2005]	1	
Infraorder Anomura H. Milne Edwards, 1832		
Superfamily Paguroidea Latreille, 1802		
Family Diogenidae Ortmann, 1892		
Paguristes mexicanus (Vega, Cosma, Coutiño, Feldmann, Nyborg, Schweitzer, and Waugh, 2001)	1	1
Superfamily Paguroidea species 1 *in* Schweitzer *et al.*, 2006 [imprint 2005]	1	
Superfamily Paguroidea species 2 *in* Schweitzer *et al.*, 2006 [imprint 2005]	1	
Superfamily Paguroidea species 3 *in* Schweitzer *et al.*, 2006 [imprint 2005]	1	
Superfamily Galatheioidea Samouelle, 1819		
Family Galatheidae Samouelle, 1819		
Subfamily Galatheinae Samouelle, 1819		
Galatheinae genus and species indet. *herein*	1	
Infraorder Brachyura Latreille, 1802		
Superfamily Homoloidea de Haan, 1839		
Family Homolidae de Haan, 1839		
Homola bajaensis new species	1	
Superfamily Raninoidea de Haan, 1839		
Family Raninidae de Haan, 1839		
Subfamily Ranininae de Haan, 1839		
Lophoranina bishopi Squires and Demetrion, 1992	1	1
Ranina berglundi Squires and Demetrion, 1992	1	
Subfamily Raninoidinae Lőrenthey and Beurlen, 1929		
Raninoides acanthocolus new species	1	
Raninoides proracanthus new species	1	
Superfamily Cyclodorippoidea Ortmann, 1892		
Family, genus and species indet. *herein*	1	
Superfamily Calappoidea H. Milne Edwards, 1837		
Family Calappidae H. Milne Edwards, 1837		
Calappilia hondoensis Rathbun, 1930b	1	1
Family Hepatidae Stimpson, 1871		
Eriosachila bajaensis Schweitzer *et al.*, 2002	1	
Prehepatus mexicanus new species	1	
Superfamily Parthenopoidea MacLeay, 1838		
Family Daldorfiidae Ng and Rodríguez, 1986		
Daldorfia salina new species	1	
Superfamily Cancroidea Latreille, 1802		
Family Atelecyclidae Ortmann, 1893		
Levicyclus tepetate Schweitzer *et al.*, 2002	1	
Family Cancridae Latreille, 1802		
Anatolikos undecimspinosus new species	1	
Family Cheiragonidae Ortmann, 1893		
Montezumella tubulata Rathbun, 1930b*	1	
Superfamily Xanthoidea MacLeay, 1838		
Family Pilumnidae Samouelle, 1819		
Lobonotus mexicanus Rathbun, 1930b	1	1
Paracorallicarcinus tricarinatus new species	1	
Family Trapeziidae Miers, 1886		
Archaeotetra inornata Schweitzer, 2005	1	
Superfamily Xanthoidea MacLeay, 1838		
Family, genus and species indet. *herein*	1	
Superfamily Goneplacoidea MacLeay, 1838		
Family Goneplacidae MacLeay, 1838		
Amydrocarcinus dantei Schweitzer *et al.*, 2002		1
Superfamily Portunoidea Rafinesque, 1815		
Family Portunidae Rafinesque, 1815		
Subfamily Carcininae MacLeay, 1838		
Genus and species indet. *herein*		1

laboratory and that care in the initial collecting of the specimens was the best assurance of conserving the specimens.

The best manner for collecting specimens under these conditions is to extract the specimens in small pieces of rock, allow them to dry thoroughly, and avoid abrading the surface. Impregnating the specimen with a dilute solution of glyptol hardens the surface sufficiently to permit the specimens to be wrapped and packed. However, nothing that was attempted was successful at removing salt crystals that obscured fine detail on the surface of the specimen.

Localities

All of the following localities are in the state of Baja California Sur, México, at localities northwest of La Paz, the state capital.

Waypoint 29: Bateque Formation, Lat. 26°57´16.1˝N, Long. 113° 03´44.6˝W, near the village of San Ignacio, collected 9 June 2003 and 11 June 2003

Waypoint 30: Bateque Formation, Lat. 26°56´31.3˝N, Long. 113° 04´13.1˝W, near the village of San Ignacio, collected 10 June 2003

Waypoint 32: Bateque Formation, Lat. 26°55´57.2˝N, Long. 113° 04´49.0˝W, near the village of San Ignacio, collected 10 June 2003

Waypoint 39: Tepetate Formation, Lat 24°19´56.8˝N, Long. 111°

1.0´6.6˝W, near the village of El Cien, collected 15 June 2003

Waypoint 70: Bateque Formation, Lat. 26°45.918´N, Long. 113°0.953´W, in a steep valley below Basalto Esperanza, collected 26 February 2002

Waypoint 72: Bateque Formation, Lat. 26°55.647´N, Long. 113°10.000´W, Isla Pelicano Norte, in Laguna San Ignacio, southwest of San Ignacio village, collected 27 February 2002.

Waypoint 75: Bateque Formation, Lat. 26°42.596´N, Long. 112°58.087´W, on the flanks of Mesa La Salina, near the village of San Ignacio, collected 28 February 2002

Systematic Paleontology

Repositories for Type and Studied Material and Institutional Abbreviations: All type material and other specimens are deposited in the Museo de Historia Natural, Universidad Autónoma de Baja California Sur, La Paz, Baja California Sur, México (MHN-UABCS). Other institutional abbreviations used include MSB, Museu Geòlogic del Seminari de Barcelona.

Order Decapoda Latreille, 1802
Infraorder Anomura H. Milne Edwards, 1832
Superfamily Galatheoidea Samouelle, 1819
Family Galatheidae Samouelle, 1819
Subfamily Galatheinae Samouelle, 1819

Genus and Species indeterminate
(Figs. 2.1, 2.2)

Material examined: 2 specimens (MHN-UABCS/Ba12-14, Ba12-15).

Occurrence: Waypoint 29.

Discussion: The material is very poorly preserved, making a description impossible, but it is clearly referable to the Galatheinae of the Galatheidae, based upon the transverse ridges on the carapace of the specimens. MHN-UABCS/Ba12-15 retains what appears to be a portion of a cervical groove, but it is too poorly preserved to be certain. MHN-UABCS/Ba12-14 may be a molt or possibly two individuals preserved together. More complete material will be necessary to confirm identification of these specimens.

Galatheines are known from Eocene rocks of Washington, USA, and Oligocene and Miocene deposits of Alaska as well as from the Cretaceous and Miocene of Japan; thus the subfamily was well-established in the Pacific by Eocene time (Schweitzer and Feldmann, 2000c). In addition, Cretaceous Gulf Coastal, USA, occurrences are known (Stenzel, 1945), so that the occurrence in Baja California could easily be explained by expansion of the North Pacific range southward or migration from the Gulf Coastal region through the open Central American Seaway (Bice *et al.*, 2000).

Infraorder Brachyura Latreille, 1802
Section Podotremata Guinot, 1977
Superfamily Homoloidea de Haan, 1839
Family Homolidae de Haan, 1839
Genus *Homola* Leach, 1815

Type species: *Homola spinifrons* Leach, 1815 (subjective synonym of *Cancer barbatus* Fabricius, 1793).

Fossil species: *Homola bajaensis* new species; *Homola vancouverensis* Schweitzer, 2001a.

Discussion: The new species is placed within *Homola*, rather than *Latheticocarcinus* Bishop, 1988, to which it is also similar, for several reasons. The new species retains portions of the subdorsal elements on both the right and left side of the carapace. Those elements in species of *Latheticocarcinus* are fragmentary if preserved at all, whereas in the other known fossil species of *Homola*, those elements are preserved (Schweitzer, 2001a). This suggests a possible differential degree of calcification of these elements between the two genera, being better calcified and thus more easily preserved in *Homola*. Species of *Homola* are known to possess well-developed spines visible in dorsal view on the subdorsal regions, and the new species clearly displays four such spines. The new species displays a bifid rostrum, well-defined carapace regions, and a rectangular hepatic region directed parallel to the cervical groove, all typical of at least some species of *Homola* (Schweitzer *et al.*, 2004a). The new species differs from species of *Latheticocarcinus* in having the cervical groove less well-defined than in species of that genus, so that it does not clearly separate the dorsal carapace into anterior and posterior portions, and the carapace in species of *Latheticocarcinus* is more flattened, both transversely and longitudinally. Schweitzer *et al.* (2004a, fig. 1) noted that *Homola* and *Latheticocarcinus* differed from one another in the path of the branchiocardiac groove; however, that groove is not well enough preserved on the new species to determine its conformation.

We note here that *Homola* and *Latheticocarcinus* share several features, including some with the new species, including a bifid rostrum in most species, pseudo-rostral spines, metabranchial ridges extending from the cardiac region in many species, regions ornamented with large tubercles, and well-developed cervical and branchiocardiac grooves. Interestingly, as it stands now, species of *Latheticocarcinus* are Cretaceous and Paleocene in age, and species of *Homola* are Eocene to Recent (Schweitzer *et al.*, 2004a), suggesting that the primary division of the genera may be based upon age. As stated first by Collins and Rasmussen (1992) and reiterated by Schweitzer *et al.* (2004a), recovery of the sternum and abdomen of fossil *Latheticocarcinus* may indeed show that the two genera are synonymous, yielding one genus with a continuous range from the Cretaceous to Recent.

This is the second Eocene occurrence of *Homola*; both are from the Pacific coast of North America. *Homola vancouverensis* is known from the Late Eocene Hoko River Formation, while the Bateque species is early or middle Eocene. Thus, the new
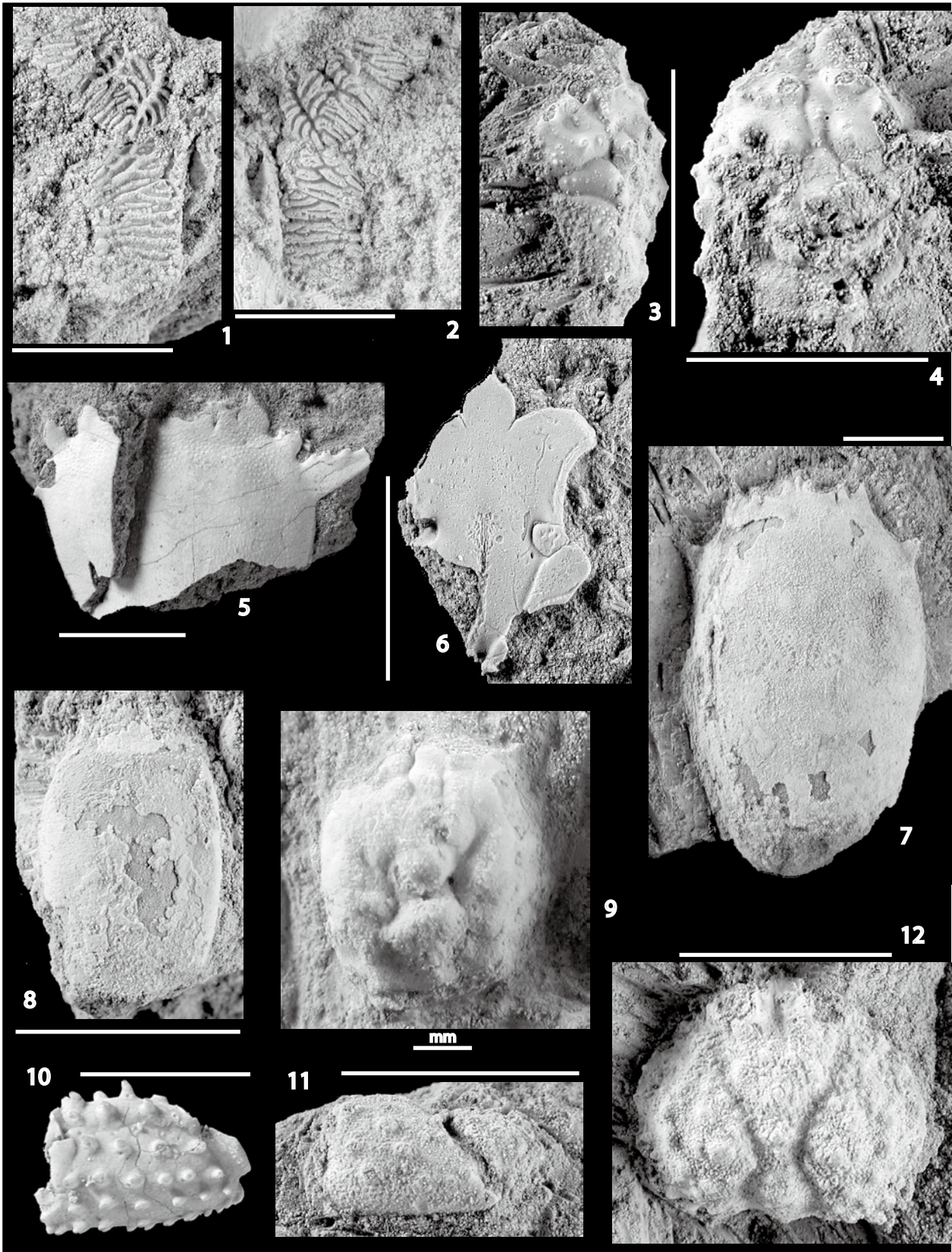
occurrence, although slightly older, does not appreciably change recent interpretations of its geological history (Schweitzer *et al.*, 2004a).

***Homola bajaensis* new species**

(Figs. 2.3, 2.4)

Diagnosis: Carapace widest just posterior to cervical groove; rostrum sulcate, spines separated to bases; subdorsal regions with well-developed spines.

Description: Carapace longer than wide (width measured between *lineae homolicae*), widest just posterior to cervical groove; *lineae homolicae* well developed; regions well-defined by grooves, regions ornamented with granules or large swellings; carapace moderately vaulted longitudinally and transversely.

Rostrum axially sulcate, bifid, spines separated to bases. Pseudo-rostral spine and orbital area damaged; appearing to have been a strong supraorbital spine based upon broken spine base. Anterolateral and posterolateral margins confluent, sinuous, defined by *lineae homolicae*.

Post-rostral region depressed, flattened. Epigastric regions large, trapezoidal, broadest side positioned along orbital area, markedly swollen centrally; protogastric region inflated, with two sharp swellings directed in oblique line parallel to cervical groove; mesogastric region with long anterior process, bearing sinuous lateral margins, region widened and with broad swelling posteriorly; metagastric region widest of axial regions, with concave upper and convex lower margins, narrowing slightly posteriorly; urogastric region narrow, depressed; cardiac region bilobate anteriorly, remainder unknown, possibly with weak metabranchial ridges extending laterally (MR of Schweitzer *et al.*, 2004a); intestinal region unknown.

Hepatic region narrow, with spine near anterolateral margin, oriented roughly parallel to cervical groove. Cervical groove deep, continuous across midline. Branchiocardiac groove broad near *lineae homolicae*. Branchial regions granular.

Subdorsal regions positioned perpendicular to dorsal carapace, spines visible in dorsal view. Subhepatic region with stout spine on anterior margin, upward-directed spine visible in dorsal view positioned along posterior border formed by sub-cervical groove. Subbranchial region separated into two triangular sections by subbranchial groove; anterior-most section with one spine positioned near *linea homolica* and visible in dorsal view; posterior-most section with one anterior and one posterior spine, each positioned near *linea homolica* and visible in dorsal view.

Etymology: The trivial name refers to Baja California Sur, the region from which the specimen was collected.

Type: The holotype and sole specimen, MHN-UABCS/Ba13-1.

Occurrence: Waypoint 30.

Discussion: The specimen is damaged, but the front, enough of the dorsal carapace, and remarkably complete subdorsal regions are preserved, making it possible to name a new species. The new species differs from the other Eocene species, *Homola*

vancouverensis, because *H. bajaensis* has less bulbous carapace regions and less sinuous lateral margins and a much larger epigastric region than *H. vancouverensis*. *Homola bajaensis* is also an order of magnitude smaller than *H. vancouverensis*, although it is similar in size to specimens of other decapods with which it was found. Interestingly, *H. bajaensis* was recovered from what have been interpreted to have been relatively shallow water, inner shelf deposits (Squires and Demetrion, 1992; Schweitzer *et al.*, 2006 [imprint 2005]); *H. vancouverensis* and the extant species of the genus are known primarily from deep-water, outer shelf and continental slope habitats (Schweitzer *et al.*, 2004a) as the foraminiferan analysis of the Bateque Formation also documents. Many species of *Latheticocarcinus* are known from epicontinental, and thus relatively shallow, areas (Schweitzer *et al.*, 2004a). If indeed it is eventually shown that *Latheticocarcinus* and *Homola* are synonymous, it is possible that *H. bajaensis* was one of the last of the lineage to inhabit shallow water environments.

Superfamily Raninoidea de Haan, 1839
Family Raninidae de Haan, 1839
Subfamily Ranininae de Haan, 1839
Genus *Ranina* Lamarck, 1801

Ranina berglundi Squires and Demetrion, 1992
(Figs. 2.5, 2.6)

Ranina berglundi Squires and Demetrion, 1992, p. 43, fig 5. 128–129.

Emendation to description: Second anterolateral spine long, stoutest at the base, directed anterolaterally. Sternum typical of the subfamily, sternites 1–3 fused, sternite 4 broad, anterior margins convex, lateral margins concave, sternite 5 poorly known, with shallow longitudinal depression.

Material examined: MHN-UABCS/Ba7-3, anterior half of dorsal carapace; MHN-UABCS/Ba10-10, anterior portion of sternum; MHN-UABCS/Ba10-9, miscellaneous carapace fragments.

Occurrence: MHN-UABCS/Ba7-3 was collected from Waypoint 70. MHN-UABCS/Ba10-9 and 10-10 were collected from Waypoint 75.

Discussion: Six specimens referable to *Ranina berglundi* were collected from the Bateque Formation at localities different from those collected by Squires and Demetrion (1992) in the same unit. The new material does not add appreciably to the description of the dorsal carapace, which was based upon four relatively well-preserved specimens. MHN-UABCS/Ba10-10, however, is a

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← Fig. 2. Decapoda: Anomura and Brachyura. 1–2, Galatheinae genus and species indeterminate, MHN-UABCS/Ba12-14, possible molt, actual specimen (1) and Exaflex® cast (2); 3–4, *Homola bajaensis* new species, holotype, MHN-UABCS/Ba13-1, lateral view showing subdorsal regions and spines (3) and dorsal carapace view (4); *Ranina berglundi* Squires and Demetrion, 1992, dorsal carapace showing second anterolateral spine, MHN-UABCS/Ba7-3 (5) and partial sternum, MHN-UABCS/Ba10-10 (6); 7, *Raninoides acanthocolus* new species, holotype, MHN-UABCS/Ba12-6, dorsal carapace; 8, *Raninoides proracanthus* new species, holotype, MHN-UABCS/Ba12-7; 9, ?Cyclodorippoidea family, genus, and species indeterminate, MHN-UABCS/Ba14-12, notice longitudinal shearing of carapace; 10–11, *Prehepatus mexicanus* new species, outer surface of manus, holotype, MHN-UABCS/Ba10-8 (10) and outer surface of manus and carpus, MHN-UABCS/Ba12-4 (11); 12, *Calappilia hondoensis* Rathbun, 1930b, dorsal carapace, MHN-UABCS/Ba14-11. Scale bars = 1 cm unless otherwise marked.

portion of a sternum typical of species of *Ranina* (Fig. 2.6) that we attribute to R. *berglundi* and that was not part of the original description and illustrations.

Subfamily Raninoidinae Lőrenthey and Beurlen, 1929
Genus Raninoides H. Milne Edwards, 1837

Raninoides H. Milne Edwards, 1837, p. 196–198.

Laeviranina Lőrenthey and Beurlen, 1929, p. 105.

Type species: Ranina laevis Latreille, 1825.

Included species: see Table 2.

Discussion: The problem of differentiation between species of *Raninoides* and *Laeviranina* has been addressed on several occasions (Feldmann, 1991; Tucker, 1998; Schweitzer *et al.*, 2000). There are no dorsal carapace, sternal, abdominal, or appendage characters that categorically can be used to determine if a species belongs to one genus or the other (Schweitzer *et al.*, 2000). For example, species had been assigned to one of the two genera based upon whether they possessed narrow orbital fissures or open orbital grooves; however, each condition occurs in some species of each genus (Schweitzer *et al.*, 2000). The character considered to be most diagnostic, presence of a postfrontal ridge in *Laeviranina* which is absent in *Raninoides*, was found to be present in some extant species of *Raninoides* (Schweitzer *et al.*, 2000). Interestingly, the new species of *Raninoides* described here possesses characters that are intermediate between the original conception of *Raninoides* and *Laeviranina*. Whereas both Feldmann (1991) and Tucker (1998) suggested that some features of the sternum could be used to differentiate the two genera, none of these could be substantiated (Tucker, 1998; Schweitzer *et al.*, 2000). Thus, we synonymize the two genera; *Raninoides* is the senior synonym.

Examination of the fossil record of the two genera shows that nearly all of the species referred to *Laeviranina* are Eocene in age, while those referred to *Raninoides* are nearly all post-Eocene, including extant species. All of the species originally referred to *Laeviranina* are extinct and possess a post-frontal ridge; it seems likely that presence of a post-frontal ridge was an early character in the lineage which persists in some species today (see Schweitzer *et*

Table 2. Species of *Raninoides*, listed from youngest to oldest. Species are listed alphabeticlly within each age bracket. List modified after Tucker (1995).

Taxon	Original Genus	Age	Location
Raninoides laevis (Latreille, 1825)	*Ranina*	Recent	Western Atlantic
R. benedicti Rathbun, 1935b	*Raninoides*	Recent	Eastern Pacific
R. bouvieri Capart, 1951	*Raninoides*	Recent	Atlantic
R. crosnieri Ribes, 1989	*Raninoides*	Recent	Madagascar
R. hendersoni Chopra, 1933	*Raninoides*	Recent	Indo-Pacific
R. lamarcki A. Milne Edwards and Bouvier, 1923	*Raninoides*	Recent	Central America
R. longifrons Chen and Türkay, 2001	*Raninoides*	Recent	Western Pacific
R. louisianensis Rathbun, 1933	*Raninoides*	Recent	Caribbean
R. personatus Henderson, 1888	*Raninoides*	Recent	Indo-Pacific
R. javanus (Böhm, 1922)	*Raninellopsis*	Miocene	Java
R. mexicanus Rathbun, 1930b (very fragmental)	*Raninoides*	Miocene	México
R. morrisi Collins et al., 2003	*Raninoides*	Miocene	Indonesia
R. rathbunae Van Straelen, 1933 (see Feldmann and Schweitzer, 2004)	*Raninoides*	Miocene	Venezuela
R. hollandica (Collins et al., 1997)	*Laeviranina*	late Oligocene	Northern Europe
R. eugenensis Rathbun, 1926	*Raninoides*	Oligocene	Oregon
R. fulgidus Rathbun, 1926	*Raninoides*	late Eocene–Oligocene	Washington–Oregon
R. oregonensis Rathbun, 1926	*Raninoides*	Oligocene	Oregon
R. budapestiniensis (Lőrenthey, 1897)	*Ranina*	late Eocene	Hungary
R. goedertorum (Tucker, 1998)	*Laeviranina*	late Eocene	Washington
R. nodai Karasawa, 1992	*Raninoides*	late middle Eocene	Japan
R. fabianii (Lőrenthey and Beurlen, 1929)	*Ranina (Laeviranina)*	middle–late Eocene	Europe
R. vaderensis Rathbun, 1926	*Raninoides*	middle–late Eocene	Pacific Northwest
R. dickersoni Rathbun, 1926	*Raninoides*	middle Eocene	California
R. perarmata (Glaessner, 1960)	*Laeviranina*	middle Eocene	New Zealand
R. pulchra (Beschin *et al.,* 1988)	*Laeviranina*	middle Eocene	Italy
R. araucana (Philippi, 1887)	*Symnista*	early Eocene	Chile
R. glabra (Woodward, 1871)	*Palaeocorystes*	early Eocene	Northern Europe
R. gottschei Böhm, 1927	*Raninellopsis*	early Eocene	England
R. notopoides (Bittner, 1883)	*Ranina*	early Eocene	England
R. sinuosus (Collins and Morris, 1978)	*Laeviranina*	early Eocene	Pakistan
R. acanthocolus new species	*Raninoides*	Eocene	Baja California
R. proracanthus new species	*Raninoides*	Eocene	Baja California
R. slaki Squires, 2001	*Raninoides*	Eocene	California
R. treldenaesensis Collins and Jakobsen, 2003	*Laeviranina*	Eocene	Denmark
R. borealis (Collins and Rasmussen, 1992)	*Laeviranina*	middle Paleocene	Greenland
R. bournei (Rathbun, 1928)	*Notosceles*	Paleocene	southcentral USA

al., 2000, for examples). Clearly there has been evolution of various characters within the lineage (again, see Schweitzer *et al.*, 2000, for examples), but retention of some of the characters that had appeared as early as the Eocene suggests that this genus is very conservative. Thus, there is no clear means to separate *Laeviranina* and *Raninoides* into two separate genera. The synonymy makes the list of referred species quite long (Table 2).

Fam and Nyborg (2003) proposed a new species of *Raninoides*, *R. bocki*, in an abstract of the 2003 Annual Meeting of the Geological Society of America. Article 13.1.1 of the International Code of Zoological Nomenclature (1999, p. 17) states that "every name published after 1930...must...be accompanied by a description or definition that states in words characters that are purported to differentiate the taxon." Further, Article 16.4.1 states that for names published after 1999, a holotype or syntypes must be designated for the new taxon. Neither requirement was met by the abstract. In addition, although not required by the Code, types of the new taxon were not illustrated (International Code, 1999, Recommendation 16F, p. 21), and the publication was in a dubious venue (International Code, 1999, Article 9.9), an abstract of a poster, although the abstracts for GSA Meetings are in fact widely disseminated. Thus, the name *Raninoides bocki* becomes a *nomen nudum* (International Code, 1999, p. 111) and is not an available name.

Raninoides acanthocolus new species
(Fig. 2.7)

Diagnosis: Carapace lacking postfrontal ridge; anterolateral spines positioned close to front of carapace about 14 percent the distance posteriorly on carapace; anterolateral spines triangular, broad, short; orbital notches very narrow; outer-orbital spines very weakly bifid; inner-orbital spine short.

Description: Carapace longer than wide, maximum width about 60 percent maximum length, position of maximum width about 37 percent the distance posteriorly on carapace, just posterior to anterolateral spine; carapace surface appearing to have been smooth, lacking a postfrontal ridge, branchiocardiac grooves appearing to have been moderately developed; carapace moderately vaulted longitudinally, highly vaulted transversely.

Front composed of three elements: rostrum and inner orbital spines; rostrum initially straight-sided at base, then converging to a triangular tip, tip axially keeled, sulcate on either side of keel; inner orbital spines short, blunt, space between rostrum and inner orbital spines broadly concave; frontal width about 30 percent maximum carapace width. Intra-orbital spine blunt, longer than inner-orbital spine, separated from inner orbital spine by narrow notch and from outer orbital spine by short, narrow notch; inner notch nearly closed along margin. Outer orbital spine about as long as rostrum, weakly bifid, outer bifurcation longest, inner bifurcation very short, area between bifurcation concave; fronto-orbital width about half maximum carapace width.

Anterolateral margin short, length about one-quarter

posterolateral length, weakly convex; anterolateral spine short, triangular, broad at base, directed anterolaterally, positioned close to front, about 14 percent the distance posteriorly on carapace. Posterolateral margin initially weakly convex posterior to anterolateral spine, then arcing axially in nearly straight segment. Posterior margin unknown.

Remainder of carapace and appendages unknown.

Measurements: Measurements (in mm) taken on the sole specimen of *Raninoides acanthocolus*: maximum carapace length = 36.1; maximum carapace width = 21.0; fronto-orbital width = 11.9; frontal width = 6.4; width between bases on anterolateral spines = 18.6; length to position of maximum width = 13.5; length to bases of anterolateral spines 5.0; length between outer orbital spines and anterolateral spine (anterolateral margin) = 7.7; length of posterolateral margin = 30.5.

Etymology: The trivial name is derived from the Greek words *kolos* meaning shortened and *akantha* meaning spine, alluding to the short orbital and anterolateral spines in the new species.

Types: The holotype and sole specimen, MHN-UABCS/Ba12-6.

Occurrence: Waypoint 29.

Discussion: The new species is unique among species in the genus in possessing extremely short orbital and anterolateral spines, much shorter than in the other species known from the Eocene of Pacific coastal North America, including *R. goedertorum* and *R. vaderensis*. In addition, the anterolateral spines are positioned very close to the front, only 14 percent the distance posteriorly, and are also shorter than in the other Eocene species. The single specimen is quite complete and reasonably well-preserved. It is also considerably larger than the specimens of other taxa found in association with it and within the same bed.

Raninoides proracanthus new species
(Fig. 2.8)

Diagnosis: Carapace small, longer than wide; anterolateral spines tiny; outer-orbital spine singular; orbits with fissures.

Description: Carapace longer than wide, maximum width about 60 percent maximum length, position of maximum width about half the distance posteriorly on carapace, carapace moderately vaulted transversely and longitudinally.

Rostrum long, axially sulcate, lateral margins parallel at base, converging slightly distally, then extending into central distal projection; broadening at base into poorly developed inner-orbital spines; front, including rostrum and inner-orbital spines, about 35 percent maximum carapace width; intra-orbital spines short, blunt, separated from inner-orbital and outer-orbital spines by fissures; outer-orbital spines long, almost as long as rostrum; fronto-orbital width about 65 percent maximum carapace width. Anterolateral and posterolateral margins confluent; anterolateral portion with very small, blunt projection just posterior to outer-orbital spine; anterolateral portions weakly convex; posterolateral portions nearly straight, converging distally.

Frontal region depressed slightly below remainder of carapace.

Carapace surface appearing to have been smooth.

Remainder of carapace and appendages unknown.

Measurements: Measurements (in mm) taken on the dorsal carapace of specimens of *Raninoides proracanthus* are as follows. MHN-UABCS/Ba12-7 (holotype): maximum carapace length = 11.8; maximum carapace width = 7.6; fronto-orbital width = 4.6; frontal width = 2.6; length to position of maximum width = 5.9. MHN-UABCS/Ba12-8 (paratype): maximum carapace length = 11.0; maximum carapace width = 6.1; fronto-orbital width = 4.0; frontal width = 2.2; length to position of maximum width = 5.4.

Etymology: The trivial name is derived from the Greek words *prora*, meaning prow or bow, and *acanthos*, meaning spine, in reference to the anterolateral spines, which are extremely short in this species.

Types: Holotype, MHN-UABCS/Ba12-7, and paratype, MHN-UABCS/Ba12-8.

Occurrence: Waypoint 29.

Discussion: Placement of the specimens of *Raninoides proracanthus* into a genus is difficult because of the incomplete nature of the material. The presence of a rostrum with inner-orbital spines, intra-orbital spines, outer-orbital spines, and two orbital fissures clearly places the material within the Raninoidinae (Tucker, 1998). It is excluded from *Notopoides* Henderson, 1888, because that genus lacks anterolateral spines altogether, has a much narrower fronto-orbital area than the new material, and has an ovate, broadened carapace not evident in the specimens referred to *R. proracanthus*. Species of *Notosceles* Bourne, 1922, are in many regards similar to the new specimens; some species possess a trifid front as in the new specimens. In addition, all species of *Notosceles* have an anterolateral spine and a post-frontal ridge. However, most species of *Notosceles* have fused orbital fissures or very short orbital fissures, while those of *R. proracanthus* are well-developed. In addition, the fronto-orbital area of species of *Notosceles* is narrower than that of the new specimens. Species referred to *Quasilaeviranina* Tucker, 1998, are generally much more ovate than the new material, and the orbital fissures of *Quasilaeviranina* are closed. Thus, the specimens are best placed within *Raninoides*, which can accommodate specimens with orbital fissures and a rather broad fronto-orbital region.

Raninoides proracanthus differs from *R. acanthocolus* new species in its much smaller size, tiny anterolateral spines, orbital fissures, trifid rostrum, and singular outer-orbital spine. *Raninoides acanthocolus* has large anterolateral spines, open orbital notches, a singular rostrum, and bifid outer-orbital spines. In addition, the fronto-orbital width of *R. acanthocolus* is considerably narrower than that of *R. proracanthus*. Because of these major differences, it is unlikely that specimens of *R. proracanthus* are juveniles of *R. acanthocolus*. The specimens of *R. proracanthus* are in the same size range as the other specimens recovered from the locality; the specimen of *R. acanthocolus* is certainly unusual in its large size.

Raninoides proracanthus is unusually small for the genus. Another very small specimen referred to *Laeviranina* sp. was recovered from Eocene rocks of Chiapas (Vega *et al.*, 2001); however, that specimen is insufficiently preserved to compare with *R. proracanthus*. *Notopus minutus* Vega *et al.*, 2001, was also described from Chiapas; although similar in size to *R. proracanthus*, that species differs in having short outer-orbital spines and a markedly granular dorsal carapace that is not seen in *R. proracanthus*.

?Superfamily Cyclodorippoidea Ortmann, 1892

Discussion: The rectangular specimen herein questionably referred to the Cyclodorippoidea is quite enigmatic. The specimen is slightly distorted as if it had been sheared, wherein the right side is slightly displaced anteriorly with respect to the left side, and the cardiac region is shifted such that it is oblique to the axis. This suggests that the distortion was the result of a weakly calcified carapace rather than being distorted due to tectonic shearing, because other specimens do not exhibit this type of carapace distortion. In any event, the distortion of the carapace and carapace regions, in addition to the damage to the front and orbital regions, makes it difficult to identify the specimen.

There is no evidence of *lineae homolicae* on either side of the carapace; quite the contrary, the lateral sides are continuous with the dorsal carapace. Thus, although the specimen exhibits a rectangular carapace and regional development reminiscent of some members of the Homolidae, it cannot be referred to that family. Members of the Homolodromiidae lack *lineae homolicae*, but they have well-developed cervical and branchiocardiac grooves that separate the carapace into three distinct regions (Schweitzer *et al.*, 2004a, fig. 6), not evident in the new specimen. In addition, homolodromiids are almost always widest in the posterior third of the carapace, exhibiting a bulbous outline of the branchial regions of the carapace, which is not evident in the new specimen.

The group to which the new specimen is most similar is the Cyclodorippoidea, especially the Cymonomidae Bouvier, 1897. Members of the superfamily are generally small (5–10 mm length), with protruding fronts, short anterior processes on the mesogastric region that terminate between the epigastric regions, and hepatic regions directed obliquely toward the axis and parallel to the cervical groove (Tavares, 1991, 1993, 1994, 1996, 1997, 1998), all evident in the new specimen. Some members have differentiated branchial regions (Tavares, 1993), and genera within the Cymonomidae exhibit a rectangular carapace (Tavares, 1990, 1994). Thus, it seems possible that the specimen may be referrable to the Cyclodorippoidea, with affinities with the Cymonomidae, but more complete, undistorted material will be necessary to test this. Interestingly, the Cymonomidae is nearly exclusively an American family in modern oceans (Tavares, 1994), and the Cyclodorippoidea has previously been reported from the Eocene of Pacific Coastal North America (Schweitzer, 2001a).

Family, genus, and species indeterminate
(Fig. 2.9)

Description of material: Carapace rectangular, longer than wide, maximum carapace width about 90 percent maximum length, transversely flattened, moderately vaulted longitudinally. Front projecting well beyond orbits, frontal width about one-quarter maximum carapace width; orbits circular, directed forward, fronto-orbital width about 80 percent maximum carapace width; anterolateral and posterolateral margins confluent, sinuous, appearing to have been a spine just anterior to intersection of cervical groove with lateral margin; posterior margin width about 60 percent maximum carapace width.

Post-frontal region axially sulcate, bulbous on either side of axis; epigastric regions square, inflated; protogastric regions inflated, not well-differentiated from other regions; mesogastric region triangular, apex terminating between epigastric regions, broadened and inflated anteriorly; urogastric region depressed well below level of other axial regions; cardiac region bulbous and rounded anteriorly, narrowing and flattening distally; intestinal region short, flattened, poorly differentiated.

Hepatic regions flattened, triangular, not well-differentiated from protogastric regions. Cervical groove best developed axially; epibranchial regions oriented at oblique angle to axis, parallel to cervical groove; mesobranchial region centrally inflated, forming a weak ridge continuous with cardiac region; metabranchial region depressed below level of other branchial regions.

Remainder of carapace, ventral aspects, and appendages unknown.

Measurements: Measurements (in mm) taken on the dorsal carapace of MHN-UABCS/Ba14-12: maximum carapace width = 4.9; maximum carapace length = 5.6; fronto-orbital width = 3.8; frontal width = 1.2; posterior width = 3.0.

Material examined: MHN-UABCS/Ba14-12.

Occurrence: Waypoint 32.

Section Heterotremata Guinot, 1977
Superfamily Calappoidea H. Milne Edwards, 1837
Family Calappidae H. Milne Edwards, 1837
Genus *Calappilia* A. Milne Edwards, 1873

Type species: *Calappilia verrucosa* A. Milne Edwards, 1873, by subsequent designation of Glaessner (1929).

Included species: Included species were recently summarized by Feldmann *et al*. (2005).

Calappilia hondoensis Rathbun, 1930b
(Fig. 2.12)

Calappilia hondoensis Rathbun, 1930b, p. 7, pl. 5, figs. 1, 2; Vega *et al*., 2001, p. 937, figs. 9–10; Schweitzer *et al*., 2002, p. 38.

Diagnosis: Carapace slightly wider than long; front straight, dorsal surface axially sulcate, about 20 percent maximum carapace width. Rostrum projected well beyond orbits, axially sulcate. Orbits circular; rimmed, rim flared upward; directed forward;

shallow; with at least one orbital fissure; outer-orbital angle produced into small triangular spine; fronto-orbital width about half maximum carapace width; with posterolateral margin initially granular, grading to spinose posteriorly and dorsal carapace ornamentation of large tubercles, some of which are roughly arranged into rows.

Emendation to description: Carapace circular, somewhat wider than long, L/W = 0.89, widest almost half the distance posteriorly on carapace; surface ornamented with large tubercles, granular between tubercles; moderately vaulted longitudinally and transversely.

Front straight, dorsal surface axially sulcate, about 20 percent maximum carapace width. Rostrum projected well beyond orbits, axially sulcate. Orbits circular; rimmed, rim flared upward; directed forward; shallow; with at least one orbital fissure; outer-orbital angle produced into small triangular spine; fronto-orbital width about half maximum carapace width. Anterolateral margin moderately convex, with small spines, spines becoming larger posteriorly, anterolateral corner just anterior to midlength of carapace; posterolateral margin nearly straight, initially granular, granules becoming larger posteriorly, ornamented with large spines posteriorly; posterior margin with short, blunt spines at posterolateral corner, blunt central larger projection, posterior width one-quarter maximum carapace width.

Protogastric regions inflated, with two or three large tubercles; bounded on outer margin by deep grooves; mesogastric region narrow anteriorly and widening posteriorly, with large tubercle posteriorly; metagastric region equant, with large central tubercle; urogastric region depressed, unornamented; cardiac region long, with three tubercles arranged in longitudinal row and several smaller, scattered tubercles, anterior-most tubercle largest; intestinal region widened posteriorly, depressed; axial regions from metagastric region to posterior margin bounded by deep lateral grooves.

Hepatic region flattened, ornamented with a few tubercles. Branchial region markedly inflated, not differentiated; ornamented with numerous tubercles, some oriented in rather ill-defined rows.

Remainder of carapace and appendages unknown.

Measurements: Measurements taken in millimeters (in mm) on specimens of *Calappilia hondoensis*: MHN-UABCS/Ba10-13, maximum carapace length (L) > 8.1; maximum carapace width (W1) = 8.6. MHN-UABCS/Ba12-22, L = 4.4; W1 = 5.1. MHN-UABCS/Ba12-25, L = 7.1; W1 = 8.2; fronto-orbital width (W2) = 4.4; frontal width (W3) = 1.9. MHN-UABCS/Te8/68-403, L = 6.2; W1 = 6.7; W2 = 4.0. MHN-UABCS/Ba14-11, L = 12.3; W1 = 13.7; W2 = 6.0; W3 = 2.4; posterior width = 3.3.

Material examined: MHN-UABCS/Ba10-13; MHN-UABCS/Ba12-22 - Ba12-25; MHN-UABCS/Ba14-10 and Ba14-11; and MHN-UABCS/Te8/68-402 and 68-403.

Occurrence: Waypoint 75 (MHN-UABCS/Ba10-13); Waypoint 29 (MHN-UABCS/Ba12-22–Ba12-25); and Waypoint 32 (MHN-UABCS/Ba14-10 and Ba14-11) in the Bateque Formation and

Waypoint 39 (MHN-UABCS/Te8/68-402 and 68-403) in the Tepetate Formation. The type specimen was collected from the Tepetate Formation at Arroyo Hondo, one kilometer from Arroyo Conejo, from which numerous other decapod specimens have been collected (Rathbun, 1930b; Schweitzer *et al.*, 2002). A specimen provisionally referred to *Calappilia hondoensis* was collected from the San Juan Formation at Cerro de Copoya, Chiapas, México (Vega *et al.*, 2001).

Discussion: The specimens are referred to *Calappilia hondoensis* based upon their granular posterolateral margin that grades to spinose posteriorly and dorsal carapace ornamentation of large tubercles, some of which are roughly arranged into rows. In addition to their morphological similarity, the new specimens were collected from the Bateque Formation, comprised of rocks of similar age, paleoenvironment, and paleoecology as the type locality for the species.

Vega *et al.* (2001) provisionally referred another specimen from Chiapas to *Calappilia hondoensis*; that specimen is very poorly preserved and more material will be necessary to confirm that assignment. In any case, the genus was well-established in Pacific coastal Mexico during the Eocene.

The new material permits description of the front and orbits, which were not preserved in the type material. In addition, we herein provide a more complete description of the anterolateral margins than was possible based upon the type material.

Family Hepatidae Stimpson, 1871

Discussion: *Prehepatus* was originally placed within the Calappidae, based upon similarities between *Prehepatus* chelae and other calappid claws (Rathbun, 1935) and subsequent authors retained this placement (Glaessner, 1969; Bishop, 1983; Fraaye and Collins, 1987). Bellwood (1996) subdivided the Calappidae *sensu lato* into several families, and in their revision of the fossil Calappoidea based upon Bellwood's work, Schweitzer and Feldmann (2000a) placed *Prehepatus* within the Hepatidae. More recently, Davie (2002, p. 117) suggested that the Hepatidae was synonymous with the Aethridae Dana, 1851, the latter of which would be the senior synonym, based upon unpublished work by he and others. Work summarized by Davie (2002) suggests that these two families are at least closely related. In another recent work, Števčić (2005) also regarded the Aethridae and Hepatidae as synonymous, and placed the Aethridae in the Parthenopoidea MacLeay, 1838. Bellwood (1996) and Martin and Davis (2001), however, had previously regarded the Hepatidae as closely related to the Calappidae *sensu stricto*, placing both families within the Calappoidea. Thus, review of these taxa is beyond the scope of this paper as it will necessitate careful examination of the Calappoidea and Parthenopoidea as well as the two families in question.

Rathbun (1935) considered *Prehepatus* claws to be similar to those of *Hepatus* Latreille, 1802, within the Calappoidea, except flattened on the upper margin to form a horizontal surface instead

of a crest (Rathbun, 1935, p. 47; Glaessner, 1969). Hepatid and calappoid claws in general are often heavily ornamented and usually have large spines on their upper margins, as seen in *Prehepatus*. In many species of *Hepatus*, the spines of the outer margin are arrayed in rows as in *Prehepatus*. The generally triangular shape of the chelae of *Prehepatus* is similar to claws of hepatid and calappoid claws. The chelae referred to *Prehepatus* differ from extant hepatids in lacking a flattened, slightly concave inner margin, which in hepatids can be brought very tightly against the anterior portion of the crab's body. Hepatid claws are usually longer proportionally than those of *Prehepatus*, and many species of hepatids have spines arrayed on a crest along the upper margin, which members of *Prehepatus* lack and instead have singular spines without a crest. Chelae referred to *Prehepatus* are quite similar to chelae that have been recovered associated with the dorsal carapace of *Hepatiscus poverelli* Vía, 1959 (MSB 15942, holotype), a confirmed member of the Hepatidae. The claws in the latter species exhibit rows of large nodes on the convex outer surface of the manus and a smoother, flattened, inner surface of the manus, nearly identical to that seen in species of *Prehepatus*. The presence of *Prehepatus*-like claws with a hepatid crab lends support to the notion that *Prehepatus* is in fact a hepatid, but it remains problematic that carapace material has yet to be found in association with *Prehepatus* chelae.

Prehepatus is primarily known from Cretaceous rocks, whereas all other fossil hepatid occurrences are Eocene or younger (Schweitzer and Feldmann, 2000a). *Prehepatus* is also unique among the Hepatidae in being represented only by chelae in the fossil record, which is perplexing given that hepatid and calappid crabs appear to have relatively durable carapaces. Members of both the Hepatidae and the related Calappidae have an excellent fossil record extending into the Eocene, based largely upon dorsal carapace material. Neither family, however, has yielded confirmed members, other than *Prehepatus*, from Cretaceous rocks. The Necrocarcinidae, long associated with the Calappoidea, has been removed to the Dorippoidea (Schweitzer *et al.*, 2003); thus, no confirmed calappoid fossils are known from the Cretaceous. If *Prehepatus* is confirmed as a member of the Hepatidae, it would extend the range of the family and its superfamily into the Cretaceous based only upon chelae and cheliped elements. Extending the range of the Hepatidae from the Eocene into the Cretaceous would have major implications for the history of the group and also for the interpretation of the survival of the Hepatidae and by implication, the Calappoidea, across the Cretaceous–Paleogene boundary. Thus, we consider the placement of *Prehepatus* within the Hepatidae as the best possible placement until a dorsal carapace can be recovered associated with claws referred to *Prehepatus*.

Genus *Prehepatus* Rathbun, 1935

Type species: *Prehepatus cretaceous* Rathbun, 1935, by page precedence in the original paper.

Other species: *Prehepatus dilksi* Roberts, 1962; *P. harrisi* Bishop, 1985; *P. hodgesi* Bishop, 1983; *P. mexicanus* new species; *P. pawpawensis* Rathbun, 1935; *P. werneri* Fraaye and Collins, 1987.

Diagnosis: Left merus triangular, with large nodes on outer surface; carpus longer than high, with nodes arranged into rows of 3 or 4 each parallel to distal margin. Right and left chelae longer than high, becoming higher distally; upper, lower, and outer surfaces ornamented with low, conical spines; proximal margin with distinctive collar, forming articulation with carpus; spines on outer surface generally arranged into rows; inner surface mostly smooth, sometimes with few small tubercles; fixed finger short, directed weakly downward with respect to lower margin of manus, with small tubercles; movable finger with small tubercles at proximal end, keel generally extending from tubercles at least half the distance of the finger.

Discussion: *Prehepatus* was erected by Rathbun (1935) to accommodate chelae collected from the Cretaceous of the Gulf Coastal Plain of North America. Subsequently, several Cretaceous species have been added, all from North America save one, *P. werneri*, from the Maastrichtian of the Netherlands (Fraaye and Collins, 1987). The genus is known only from both right and left chelae; no carapace material has ever been found in close association with the claws. The new species described herein contains the first notice of articles of the cheliped other than chelae.

Prehepatus mexicanus new species
(Figs. 2.10, 2.11)

Diagnosis: Left merus triangular, with large nodes on outer surface; left carpus with nodes arranged into rows on outer surface; left manus longer than high, outer surface convex, inner surface flattened; proximal margin oblique, with collar; lower margin with double row of tubercles; upper margin with three rows of spines; outer surface with four parallel rows of sharp spines.

Description: Left merus triangular, slightly longer than high, H/L about 0.90; upper surface with small spines; proximal margin at about 80 degree angle to upper margin; distal margin, which occludes with carpus, at about 60 degree angle to upper margin; outer surface with large spherical tubercles.

Left carpus longer than high, H/L about 0.60, highest centrally; proximal margin at about 120 degree angle to weakly convex upper margin; lower margin straight; distal margin at about 100 degree angle to upper margin; outer surface with large spherical nodes arranged into rows parallel to proximal margin, each row with 3 or 4 nodes.

Left manus longer than high, highest distally; outer surface convex; inner surface flattened. Proximal margin oblique, oriented at 60 degree angle to lower margin, with circular collar centrally, collar forming articulation with carpus, collar itself directed toward inner surface. Lower margin convex, with double row of small tubercles, inner-most row composed of smaller tubercles than outer-most. Upper margin convex; with three rows of long, sharp

spines; central row directed straight up; outer row directed laterally outward; inner row directed laterally inward. Distal margin straight, oriented at about 85 degree angle to lower margin, thickened. Outer surface with four parallel rows of sharp, long spines; lower-most row with nine spines; middle two rows with six spines each; upper most row with four spines; surface between spines smooth. Inner surface with some irregular, small granules centrally, central-most area weakly inflated.

Measurements: Measurements (in mm) taken on specimens of *Prehepatus mexicanus* new species, measurements on manus are taken on MHN-UABCS/Ba10-8, MHN-UABCS/Ba14-4, and MHN-UABCS/Ba12-3 respectively: maximum length of manus, 11.0, 9.6, 7.7; maximum height of manus, 7.4, 4.8, 4.0; height of manus just distal to proximal margin (Ba10-8), 5.0; length of fixed finger (Ba14-4, Ba12-3), 4.3, 3.0. Carpus and merus measurements from MHN-UABCS/Ba12-4: length of carpus 7.0; height of carpus, 4.3; length of merus, 3.6; height of merus, 3.3. All are left chelae.

Etymology: The new species is named for its occurrence in México.

Types: The holotype, MHN-UABCS/Ba10-8; three paratypes, MHN-UABCS/Ba12-3, MHN-UABCS/Ba12-4, MHN-UABCS/Ba14-4.

Occurrence: Waypoints 75 (MHN-UABCS/Ba10-8), 29 (MHN-UABCS/Ba12-3 and Ba12-4), 32 (MHN-UABCS/Ba14-4).

Discussion: *Prehepatus mexicanus* new species is based upon four specimens which are reasonably well-preserved. MHN-UABCS/Ba12-4 only includes the merus and carpus, but the nodes arranged into rows are of the same general shape and size as those on the mani, which clearly indicate they are conspecific. MHN-UABCS/Ba12-3 exhibits primarily an inner surface of the manus; the upper margin and the little that can be seen of the outer surface clearly show the long spines on those surfaces that are seen on the holotype. Thus, all of the material is confidently referred to the new species. The chelae clearly exhibit characters of the manus that place them within *Prehepatus*, including the collar on the oblique proximal margin, rows of spines on the outer surface, spines along the upper and lower margins, and a mostly smooth inner surface. *Prehepatus mexicanus* differs from all others species in the genus in having very well-ordered rows of slender spines on the outer surface and three rows of spines on the upper surface. Other species, such as *P. harrisi*, have stout spines on the outer surface that are arranged into rows that are less straight and are subparallel to one another (Bishop, 1985; Vega *et al.*, 1995). *Prehepatus werneri* has a more granular outer surface than *P. mexicanus* and lacks the long spines on the upper margin that characterize *P. mexicanus*. The tubercles on the outer surfaces of *P. pawpawensis* and *P. cretaceous* are arranged into much less orderly rows than in other species of the genus.

This new species marks the first notice of *Prehepatus* in Eocene rocks; all other reports have been in Cretaceous deposits.

Superfamily Parthenopoidea MacLeay, 1838
Family Daldorfiidae Ng and Rodríguez, 1986
Genus *Daldorfia* Rathbun, 1904

Type species: *Cancer horridus* Linnaeus, 1758, by orignal designation.

Included species: *Daldorfia horrida* (Linnaeus, 1758), as *Cancer*, extant; *D. bouvieri* (A. Milne Edwards, 1869), as *Parthenope*, extant; *D. fabianii* Beschin *et al.*, 2001, Oligocene; *D. garthi* Glassell, 1940, extant; *D. himaleorhaphis* Schweitzer, 2001a, Oligocene; *D. investigatoris* (Alcock, 1895), as *Parthenope*, extant; *D. leprosa* (Nobili, 1905), extant; *D. nagashimai* Karasawa and Kato, 1996, late Miocene; *D. rathbuni* (de Man, 1902), as *Thyrolambrus*, extant; *D. semicircularis* (Flipse, 1930), as *Parthenope*, extant; *D. spinosissima* (A. Milne Edwards, 1862), as *Parthenope*, extant; *D. triangularis* Sakai, 1974, extant; *Daldorfia* sp. *in* Karasawa and Kato, 1996, late Miocene; *Daldorfia* sp. *in* Kato, 2002, late Miocene.

Diagnosis: Carapace triangular; anterolateral spine typically drawn out into acute termination; regions well defined as distinct swellings; rostrum short; front downturned, sulcate; surface typically nodose or spinose. Basal antennal segment strong (modified from Glaessner, 1969; Sakai, 1976).

Discussion: Distinction between species of *Daldorfia* and *Parthenope* is difficult due to the ranges of shape and ornamentation exhibited within each genus. However, the combination of a distinctly triangular outline produced by the large anterolateral spines, the strongly inflated regions and relatively deeply incised grooves, and the downturned, sulcate front comprise a plexus of characters exhibited by species of *Daldorfia*.

Daldorfia salina new species
(Figs. 3.1–3.3)

Diagnosis: Carapace small for genus, front very deeply sulcate and downturned; distinctly triangular in outline; carapace grooves well-defined; nodose sculpture strong.

Description: Carapace tiny, triangular in outline, maximum carapace length 75% maximum width; strongly areolated, regions well defined as swellings separated by deeply depressed areas.

Front narrow, 18% maximum width measured at anterolateral corners, apparently truncate but poorly preserved. Orbits poorly preserved, fronto-orbital width approximately 35% maximum width; orbits directed anterolaterally. Anterolateral margin long, sinuous, with reentrants where cervical groove and groove separating epibranchial and mesobranchial regions intersect margin; terminating in acute, nodose anterolateral spine directed laterally. Posterolateral margin short, sinuous, straight distally and strongly convexly curving around metabranchial region. Posterior margin poorly preserved, appearing straight, about 30% maximum width.

Frontal area broadly sulcate, sloping anteriorly onto rostral surface, bounded laterally by large protogastric swellings rising to acute tip. Mesogastric region an axial dome that is less prominent

than protogastric swellings. Metagastric and urogastric regons not distinguished from one another, narrower than mesogastric region, arched. Cardiac region a prominent dome with acute tip situated posterior to midpoint of region. Hepatic region not well preserved. Epibranchial region triangular, depressed below general surface of carapace; bounded by cervical groove extending anterolaterally and by transverse depression at level of posterior end of protogastric region. Mesobranchial and metabranchial regions defined by two swellings separated by shallow depression extending posterolaterally.

External surface of cuticle not preserved; however, surface of mold of the interior of the carapace appears to be nodose. Remainder of organism not preserved.

Etymology: The trivial name refers to Mesa La Salina which is a prominent landmark situated south from the locality from which the specimens were collected.

Types: The holotype, MHN-UABCS/Ba12-26, and three paratypes, MHN-UABCS/Ba12-27 to Ba12-29.

Occurrence: Waypoint 29.

Discussion: The species that most closely resembles *Daldorfia salina* in overall form is the type species, *D. horrida*, which is a widespread species in the Indo-Pacific region (Sakai, 1976). *Daldorfia horrida* has a distinctly triangular outline, has a very strongly developed anterolateral spine which accents the triangular outline, strongly bulbous regions, deep grooves surrounding the epibranchial region, and similar relative development of the axial regions. All of these features are also characteristic of the new species. However, the two differ because the sculpture on *D. horrida* is coarser and the overall size of that species is much greater than *D. salina*. The difference of development of surface sculpture may be a result of the total loss of cuticle on the fossils. As with the other fossils collected from the low-lying exposures surrounding Laguna San Ignacio, the specimens are extremely fragile and what cuticle adheres to the molds on the interior of the carapace is probably the remains of endocuticle which exhibits very little surface detail. There is some indication of the presence of nodes or spines on the surface of the specimens and around their margins; however, there is not sufficient detail to be certain.

Daldorfia salina differs from the other two species known from carapace material in the fossil record. Both *D. himaleorhaphis* Schweitzer, 2001a, and *D. nagashimai* Karasawa and Kato, 1996, are less distinctly triangular and both exhibit less sulcate frontal regions and less distinct carapace furrows than either the type species or the new species.

The occurrence of *Daldorfia* in the Eocene Bateque Formation is the oldest occurrence of the genus and the family in the fossil record. Previously, the oldest occurrence was in the Oligocene Makah Formation in Washington State, U.S.A. (Schweitzer, 2001a). The previously hypothesized pattern of origin along the Pacific coast of North America in the Paleogene and subsequent dispersal into the western Pacific in the Neogene (Karasawa and Kato, 1996; Schweitzer, 2001b; Kato, 2002) is supported by the

new occurrence.

Superfamily Cancroidea Latreille, 1802

Family Cancridae Latreille, 1802

Subfamily Cancrinae Latreille, 1802

Genus *Anatolikos* Schweitzer and Feldmann, 2000b

Type species: *Cancer japonicus* Ortmann, 1893, by original designation.

Other species: *Anatolikos itoigawai* (Karasawa, 1990); *A. tumifrons* (Yokoya, 1933); *A. undecimspinosus* new species.

Diagnosis: Carapace wider than long, maximum length about 70–80 percent maximum carapace width, widest at position of penultimate or last anterolateral spine, about three-quarters the distance posteriorly; regions moderately defined, especially protogastric and axial regions; surface granular; front projected beyond orbits, with five coalesced spines; orbits rimmed, with two fissures, fronto-orbital width between 30–50 percent maximum carapace width; anterolateral margins convex, with 10–12 spines, some occurring in pairs; posterolateral margin nearly straight or concave, rimmed; manus of cheliped short, outer surface with three granular ridges (after Schweitzer and Feldmann, 2000b).

Discussion: The specimens here referred to the new species of *Anatolikos* conform in all regards to the diagnosis, at least in the features that are preserved, except one: possession of anterolateral spines in triads and a pair whereas the other species of the genus have paired and singular anterolateral spines. *Anatolikos* is the only genus within the Cancridae that can accommodate specimens with eleven anterolateral spines. Because the specimens at hand are incomplete, missing the front which contains important diagnostic characters within the Cancridae, and because there exists only the one difference in the anterolateral spines, we place the specimens in *Anatolikos* rather than erecting a new genus to accommodate them. Recovery of specimens with a preserved front could help confirm their placement in *Anatolikos*.

Anatolikos undecimspinosus new species

(Figs. 3.4, 3.5)

Diagnosis: Carapace wider than long, maximum length about 70 percent maximum width, widest at position of last anterolateral spines, about 70 percent the distance posteriorly; frontal width about 40 percent maximum carapace width; fronto-orbital width about half maximum carapace width; anterolateral margins with eleven spines not including outer-orbital spines; anterior-most spines in three groups of three, posterior-most spines a pair; each triad and pair separated by closed fissure visible on dorsal and ventral surface; posterolateral margin concave, anteriorly rimmed.

Description: Carapace wider than long, maximum length about 70 percent maximum width, widest at position of last anterolateral spines, about 70 percent the distance posteriorly; regions moderately defined, groove delimiting outer margin of protogastric region and axial urogastric region especially deep; moderately vaulted longitudinally, weakly vaulted transversely.

Front unknown, frontal width about 40 percent maximum carapace width. Orbits circular, fronto-orbital width about half maximum carapace width. Anterolateral margins with eleven spines not including outer-orbital spines; anterior-most spines in three groups of three, posterior-most spines a pair; spines in first triad small, blunt, curving forward; spines in second triad slightly longer than those in first triad, sharp, directed anterolaterally; spines in third triad longest of all spines, sharp, directed anterolaterally; spines in final pair small, directed laterally, second spine in pair smallest of all anterolateral spines; each triad and pair separated by closed fissure visible on dorsal and ventral surface. Posterolateral margin concave, anteriorly rimmed. Posterior margin about equal in width to fronto-orbital width.

Protogastric regions arcuate, ornamented with large tubercles and granules anteriorly and axially; orbital region broad, granular; mesogastric region with long anterior process, widened posteriorly, barely differentiated from inflated urogastric region; remainder of axial regions unknown.

Hepatic region divided into three broad swellings, axial-most is most inflated, others are essentially subdivisions resulting from fissures separating anterolateral spine triads and pair. Branchial region with inflated epibranchial area; remainder of branchial regions undifferentiated; appearing to have been granular posteriorly.

Measurements: Measurements (in mm) taken on the holotype (MHN-UABCS/Ba12-9) of *Anatolikos undecimspinosus*: maximum carapace width = 32.0; maximum carapace length = 22.4; frontal width = 12.6; fronto-orbital width = 16.2; length to position of maximum carapace width = 16.1.

Etymology: The trivial name refers to the presence of eleven anterolateral spines on the dorsal carapace, an unusual number for the family.

Types: The holotype, MHN-UABCS/Ba12-9, and paratypes, MHN-UABCS/Ba12-10 and Ba12-11.

Occurrence: Waypoint 29.

Discussion: The new species differs from all species of *Anatolikos*, and all members of the Cancrinae, in having triads of anterolateral spines. *Lobocarcinus* of the Lobocarcininae Beurlen, 1930, can have anterolateral spines arranged into triads, but members of that genus generally have seven anterolateral lobes that are bifurcate or trifurcate, are much wider than long, have marked, nodose dorsal carapace ornamentation, and spined posterolateral margins (Schweitzer and Feldmann, 2000b), all of which the new species lacks.

The placement of *Anatolikos undecimspinosus* in the genus extends both the geologic and geographic range. Previously, the genus was known from the Miocene to Recent of Japan; the occurrence in the Bateque Formation extends the genus into the Eocene of the eastern Pacific, its earliest known occurrence. The genus exhibited a North Pacific distribution, common among decapods during the Eocene (Schweitzer, 2001b), and remains endemic to that region, known only from Japan in modern oceans.
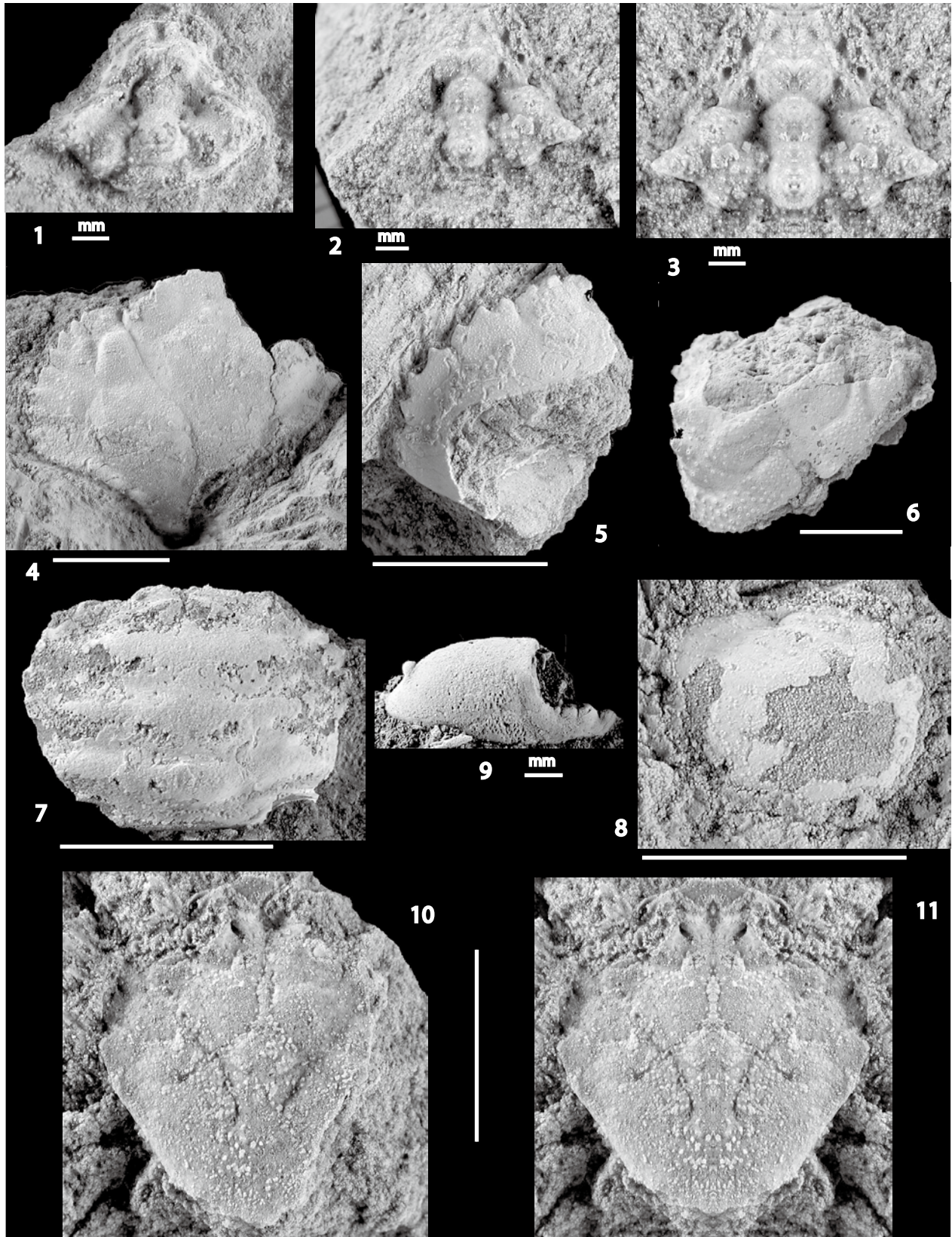
Superfamily Xanthoidea MacLeay, 1838

Family Pilumnidae Samouelle, 1819

Genus *Lobonotus* A. Milne Edwards, 1864

(= *Archaeopilumnus* Rathbun, 1919)

***Lobonotus mexicanus* Rathbun, 1930b**

(Fig. 3.6)

Lobonotus mexicanus Rathbun, 1930b, p. 2, pl. 1; Schweitzer et al., 2002, p. 20, figs. 21, 22.

Measurements: The specimen is approximately 25 mm wide and 23 mm long; however, the specimen retains only part of the dorsal carapace. These measurements only provide an approximation of the size of the specimen.

Material examined: Specimen MHN-UABCS/Ba10-11.

Occurrence: Waypoint 75.

Discussion: The sole specimen of *Lobonotus mexicanus* recovered from the Bateque Formation is fragmentary, retaining a small portion of the left anterolateral and posterolateral margins as well as part of the dorsal carapace. The sharp anterolateral spines; the broad carapace; the shape of the preserved carapace regions; and the granular ornamentation suggest that the specimen belongs to *Lobonotus mexicanus*. In that species, the carapace is granular; the anterolateral margins possess strong, sharp spines; and the carapace is broadly hexagonal. In the absence of other data, it seems best to assign the specimen to *Lobonotus mexicanus* until more complete material is collected. The species has previously been reported from the Eocene Tepetate Formation (Rathbun, 1930b; Schweitzer *et al.*, 2002).

Genus *Paracorallicarcinus* Tessier, Beschin,
Busulini, and De Angeli, 1999

Type species: *Paracorallicarcinus arcanus* Tessier, Beschin, Busulini, and De Angeli, 1999, by monotypy.

Other species: *Paracorallicarcinus tricarinatus* new species.

Diagnosis: Carapace wider than long, maximum length about 80 percent maximum width; front broad, entire, convex, at least half maximum carapace width; fronto-orbital width broad, 80–95 percent maximum carapace width; anterolateral margins with two or three spines excluding outer-orbital spines; posterolateral reentrants large, very well-developed; carapace with two or three transverse ridges.

Discussion: The affinities and family-level placement of *Paracorallicarcinus* are not straight forward. *Paracorallicarcinus* was originally described as being quite similar to *Corallicarcinus* Müller and Collins, 1991 (Tessier *et al.*, 1999). The latter genus is quite different from *Paracorallicarcinus*, however, in possessing a much narrower frontal and fronto-orbital width, about 30 percent and 60 percent respectively, in *Corallicarcinus*. Additionally, the carapace of *Corallicarcinus* is markedly hexagonal, while that of *Paracorallicarcinus* is rectangular. The carapace of *Corallicarcinus* narrows markedly posteriorly and does not appear to possess large posterolateral reentrants (Müller and Collins, 1991, pl. 7, fig. 4),

whereas the carapace of *Paracorallicarcinus* does not narrow markedly posteriorly and has large posterolateral reentrants.

Paracorallicarcinus appears to be quite similar to *Daragrapsus* Müller and Collins, 1991. *Daragrapsus* exhibits a rectangular carapace; three anterolateral spines; a broad, entire front; marked, rimmed posterolateral reentrants; and a broad fronto-orbital width as in *Paracorallicarcinus*. However, *Daragrapsus* possesses four dorsal carapace ridges that are of a different shape and configuration than that of *Paracorallicarcinus*, and the orbits of *Daragrapsus* are more poorly developed than those of *Paracorallicarcinus* and lack a rim as seen in *Paracorallicarcinus*. The similarities between the two genera suggest that they belong to the same family.

Karasawa and Kato (2003) suggested that both *Maingrapsus* Tessier *et al.*, 1999, and *Paracorallicarcinus* were similar to the extant genus *Georgeoplax* Türkay, 1983. The two fossil genera do appear to have several features in common with *Georgeoplax*, including a broad, entire front occupying between 50 and 60 percent maximum carapace width; a broad fronto-orbital width occupying between 80 and 95 percent maximum carapace width; a rectangular carapace about 80 percent as long as wide; anterolateral margins with spines or blunt projections; a front forming a "shelf" over the antennules (in *Georgeoplax* and *Paracorallicarcinus* at least); and shallow, oblique orbits. Unfortunately, none of the fossil specimens possesses the sternum or abdomen for comparison with *Georgeoplax*, but in terms of the dorsal carapace, the two fossil genera are certainly very similar to it. Thus, *Paracorallicarcinus*, *Maingrapsus*, and *Daragrapsus* are each likely related to *Georgeoplax*.

The family level placement of *Georgeoplax* has been problematic. Karasawa and Kato (2003) placed the genus within the Pilumnidae. Davie (2002) placed *Georgeoplax* within the Chasmocarcininae Serène, 1964, of the Goneplacidae MacLeay, 1838, whereas Türkay (1983), who erected the genus, did not place it into a family at all. Most authors consider the Chasmocarcininae to possess a supplementary plate between sternites 7 and 8 that covers the genital groove in males (Felder and Rabalais, 1986; Schweitzer and Feldmann, 2001). Türkay (1983, p. 101) gave no indication that such a plate existed in males, although he did describe the penis as being "situated in a groove." Members of other subfamilies within the Xanthoidea, such as the Planopilumninae, possess such a groove, apparently without a supplementary plate (Serène, 1984). Thus, it is not clear whether

← Fig. 3. Decapoda: Brachyura. 1–3, *Daldorfia salina* new species: 1, dorsal carapace showing well-preserved sulcate front, MHN-UABCS/Ba12-27, 2, partial carapace, holotype, MHN-UABCS/Ba12-26, and 3, reconstruction of MHN-UABCS/Ba12-26 using mirror image reversal process in Photoshop®, indicating shape of entire carapace, especially the long anterolateral spines; 4–5, *Anatolikos undecimspinosus* new species, dorsal carapace, holotype, MHN-UABCS/Ba12-9 (4) and subdorsal regions showing sutures between triads and pairs of spines, MHN-UABCS/Ba12-11 (5); 6, *Lobonotus mexicanus* Rathbun, 1930b, partial dorsal carapace, MHN-UABCS/Ba10-11; 7–8, *Paracorallicarcinus tricarinatus* new species, dorsal carapace showing three anterolateral spines, holotype, MHN-UABCS/Ba14-5 (7) and dorsal carapace with well preserved front, MHN-UABCS/Ba12-21 (8); 9, Superfamily Xanthoidea, family, genus, and species indeterminate, outer surface of chela, MHN-UABCS/Ba10-12a; 10–11, Subfamily Carcininae genus and species indeterminate, MHN-UABCS/Ba12-12, partial dorsal carapace (10) and reconstruction using mirror image reversal process in Photoshop® (11). Scale bars = 1 cm unless otherwise marked.

Georgeoplax is actually a member of the Chasmocarcininae. In terms of the dorsal carapace, *Georgeoplax* falls outside the range given for a broad range of characters of the Chasmocarcininae, including various length and width ratios and the shape of the orbits and the front (Schweitzer and Feldmann, 2001).

Placement of *Georgeoplax* and the three apparently related fossil genera within the Pilumnidae is the best family-level assignment at this time. The subfamily with the most similar range of dorsal carapace characters to *Georgeoplax* is the Rhizopinae, which can accommodate the broad front and ridged dorsal carapace. Unfortunately, the fossils, because they lack sterna and abdomina, cannot help to resolve the family level placement.

Paracorallicarcinus is known only from Eocene rocks of the Tethyan region. The type species, *P. arcanus*, was described from middle Eocene rocks of Italy (Tessier *et al.*, 1999), and the new species is recorded from middle Eocene rocks of Pacific Coastal México. It seems likely that the genus exhibited a Tethyan dispersal pattern, but it is not possible to determine where it originated.

Paracorallicarcinus tricarinatus new species
(Figs. 3.7, 3.9)

Diagnosis: Carapace with three pronounced transverse grooves; orbits well-defined; fronto-orbital width over 90 percent maximum carapace width; anterolateral margins with three spines excluding outer-orbital spines.

Description: Carapace wider than long, length about 80 percent maximum width; carapace regions poorly defined; ornamented by three pronounced transverse ridges; carapace moderately vaulted longitudinally and transversely.

Frontal margin extremely broad, about 60 percent maximum carapace width, convex, entire, produced in advance of orbits. Orbits oblique, directed anterolaterally, shallow, with broad, weak rim; outer-orbital spine triangular, sharp, directed forward; fronto-orbital width about 94 percent maximum carapace width. Anterolateral margin with three sharp spines not including outer-orbital spine; first spine largest, broad, triangular, directed weakly anterolaterally; second spine shorter, triangular, directed anterolaterally; last spine smallest, directed laterally. Posterolateral margin sinuous, about as long as anterolateral margin; posterolateral reentrants very large, rimmed; posterior margin rimmed, nearly straight, about 43 percent maximum carapace width.

Frontal region axially sulcate, inflated weakly on either side of axis. Epigastric regions rectangular, inflated, with sharp transverse crest along anterior margin. Protogastric and hepatic regions confluent, with broad transverse ridge extending axially from base of first anterolateral spine, ridge not crossing axis. Mesogastric region not well delimited, with long anterior process that interrupts hepatic/protogastric ridge; posterior-most portion of mesogastric region inflated, forming central portion of second broad transverse ridge extending from bases of second and third anterolateral spines

across epibranchial area and mesogastric region. Urogastric region very small and poorly defined, essentially a broad groove. Cardiac region inflated, forming central portion of third broad transverse ridge extending from posterolateral margin across branchial regions and cardiac region. Intestinal region and posterior-most branchial regions depressed well below level of transverse ridges.

Remainder of carapace and appendages unknown.

Measurements: Measurements (in mm) taken on specimens of *Paracorallicarcinus tricarinatus* new species. MHN-UABCS/Ba14-5 (holotype): maximum carapace length (L) = 11.3; maximum carapace width (W) = 14.1; fronto-orbital width (FOW) = 12.5; frontal width (FW) = 9.3; posterior width (PW) = 6.8. MHN-UABCS/Ba12-19 (paratype): L = 8.1; W = 10.3; FOW = 10.0; FW = 6.0; PW = 4.8. MHN-UABCS/Ba13-3 (paratype): L = 6.5; W = 7.8; FOW = 7.4; FW = 4.9; PW = 3.8.

Etymology: The trivial name is derived from the Latin words *carinatus*, meaning keeled, and *tri-*, meaning thrice, referring to the three prominent dorsal carapace ridges typical of this species.

Types: Holotype, MHN-UABCS/Ba14-5, and paratypes MHN-UABCS/Ba12-16 to Ba12-21, MHN-UABCS/Ba13-2 and Ba13-3, and MHN-UABCS/Ba14-6 to Ba14-9.

Occurrence: Waypoint 29 (MHN-UABCS/Ba12-16 to Ba12-21), Waypoint 30 (MHN-UABCS/Ba13-2 and Ba13-3), Waypoint 32 (MHN-UABCS/Ba14-5 to Ba14-9).

Discussion: This species appears to be the most abundant among the specimens collected from the waypoints studied here. Often, the specimens are fragmentary, but they usually retain enough of the cuticle and the diagnostic dorsal keels to indicate that they belong to the species. Unfortunately, the ventral surface and appendages are unknown for this species.

Superfamily Xanthoidea, family, genus, and species indeterminate
(Fig. 3.9)

Description of material: Manus longer than high, highest distally; bulbous; smooth. Outer surface very convex; inner surface weakly inflated. Proximal margin rounded, very short; with blunt, proximally-directed spine at upper corner. Lower margin convex, smooth; upper margin smoothly arcuate, with blunt, proximally-directed tubercle about one-quarter the distance distally from proximal margin; distal margin nearly straight, at about 90 degrees to upper margin. Fixed finger narrowing distally, curving inward, with large blunt teeth on occlusal surface, inner and outer surfaces with setal pits.

Measurements: Measurements (in mm) taken on the chelae. MHN-UABCS/Ba10-12a, length of manus = 7.7, length of manus with fixed finger = 10.9, height = 5.5; MHN-UABCS/Ba10-12b, length of manus = 5.8, length of manus with fixed finger = 7.7, height = 4.0.

Material examined: MHN-UABCS/Ba10-12a and b.

Occurrence: Waypoint 75.

Discussion: The specimens are referred to the Xanthoidea;

however, it is not possible to place the specimens within a family. One other taxon with similar chelae is known from the Bateque Formation, *Lobonotus mexicanus*, discussed above. Both the chelae of *L. mexicanus* and the chelae described here have a blunt tubercle on the proximal upper margin. Chelae of *L. mexicanus* are large with sharp, pointed fingers; granular on the outer surface; and very much larger than the chelae described here (Rathbun, 1930b; Schweitzer *et al*., 2002). It is possible that the chelae described here are conspecific, but the differences seem too great. *Amydrocarcinus dantei* Schweitzer *et al*., 2002, a member of the Goneplacidae, has smooth claws similar to the chelae described here, but chelae of *A. dantei* are much longer and have much longer, more slender fingers.

The two chelae described here have a similar form and ornamentation to many taxa within the Xanthoidea, including members of the Platyxanthidae Guinot, 1977; Panopeidae Ortmann, 1893; and Oziidae Dana, 1851. They are particularly similar to those of *Ozius* H. Milne Edwards, 1834, and *Platyxanthus* A. Milne Edwards, 1863 (see Rathbun, 1930a). Thus, we are quite confident that they belong within the Xanthoidea, but we cannot place them within a family.

<center>Superfamily Portunoidea Rafinesque, 1815
Family Portunidae Rafinesque, 1815
Subfamily Carcininae MacLeay, 1838</center>

Discussion: The subfamily as currently recognized recently has been suggested to be polyphyletic (Von Sternberg and Cumberlidge, 2001). We consider the family in the sense of Christiansen (1969), Glaessner (1969), Apel and Spiridonov (1998), and Davie (2002), as one lineage, until each subfamily can be reevaluated based upon fossil and extant occurrences.

<center>**Genus and species indeterminate**
(Figs. 3.10, 3.11)</center>

Description of material: Carapace about as long as wide, widest at position of penultimate anterolateral spine, about 40 percent the distance posteriorly; regions well-marked; carapace flattened longitudinally and transversely.

Front projected beyond orbits, axially notched, appearing to have had at least four spines, spines sharp, triangular, frontal width at least one-quarter maximum carapace width. Orbits appearing to have been rather wide, fronto-orbital width apparently about 80 percent maximum carapace width. Anterolateral margins short; nearly parallel to axis; with at least three, blunt spines; last spine smallest. Posterolateral margin longer than anterolateral margin, converging posteriorly, with small node anteriorly, followed by thickened rim, then nearly straight and without rim. Posterior margin unknown, narrow.

Epigastric regions square, inflated; protogastric regions inflated centrally; mesogastric region with long anterior process, widened anteriorly, posterior margin arcuate; metagastric region narrowing posteriorly, anterior and posterior margins concave, lateral margins

straight and converging posteriorly; urogastric region narrow, lateral and anterior margins concave, posterior margin not well differentiated from inflated cardiac region; intestinal region long, narrow, flattened.

Hepatic region inflated centrally; subhepatic region small, depressed below level of hepatic region; epibranchial region weakly arcuate, inflated; remainder of branchial regions flattened, undifferentiated.

Ventral aspect of carapace and appendages unknown.

Measurements: Measurements (in mm) taken on MHN-UABCS/Ba12-12: maximum width = 13.0; maximum length >13.0; fronto-orbital width = 10.4 (estimated); frontal width = 3.3 (at least).

Material examined: Two specimens, MHN-UABCS/Ba12-12 and Ba12-13.

Occurrence: Waypoint 29.

Discussion: The specimens at hand are similar to species of several genera within the Carcininae, including *Miopipus* Müller, 1984; *Portumnus* Leach, 1814; and *Xaiva* MacLeay, 1838. Each of these genera is about as long as wide with the position of maximum width occurring anterior to the midlength; has a short anterolateral margin with four or so anterolateral spines and a long posterolateral margin; and has a long intestinal region, each of which occur in the Bateque specimens. However, the two Bateque specimens have poorly preserved fronts, orbits, and anterolateral margins, making it impossible to assign them to a genus. Because of the poor preservation, we refrain from referring the specimens to a new genus or species until better preserved material can be collected that will permit more direct comparison to existing genera.

The specimens exhibit some similarities with members of the Pirimelidae Alcock, 1899, including the approximately equal carapace length and width; spined anterolateral margins; and a long intestinal region as in *Sirpus* Gordon, 1953. However, in the pirimelids, the point of maximum width occurs at about the midlength, the anterolateral margins are distinctly at an angle to the axis instead of nearly parallel to it as in the Bateque specimens, and the anterolateral and posterolateral margins are about equal in length. Thus, the Carcininae seems to be the best placement for the specimens at this time.

<center>**Paleobiogeography and Paleoecology**</center>

Paleobiogeography: The new taxa described here from the Bateque Formation display the same general patterns of origin and dispersal as have been described previously for decapods of the region (Schweitzer, 2001b; Schweitzer *et al*., 2002). Several of the taxa appear to have had their first occurrence in the North Pacific Ocean. These include *Homola*, *Anatolikos* and the Cancrinae, *Daldorfia* and the Daldorfiidae, and the Cyclodorippoidea. The oldest known occurrences of *Homola* are those recorded by Schweitzer (2001a) and the species described herein. The new species of *Anatolikos* extends its range into the Eocene, joining the Eocene occurrence of *Anisospinos* Schweitzer and Feldmann,

2000b, in the Hoko River Formation of Washington, USA, for the oldest occurrences of the subfamily Cancrinae. *Anatolikos* subsequently dispersed to Japan, where it is extant, a North Pacific dispersal pattern. The new species of *Daldorfia* is the oldest known occurrence of the genus and the family. Finally, the Cyclodorippoidea is already represented by an Eocene occurrence in the North Pacific; thus, if the specimen herein questionably referred to that superfamily is confirmed as a member it will not extend its range.

Prehepatus has previously been reported from the Cretaceous of the North Atlantic, Western Interior, Tethys, and Central Americas, so the new occurrence does not expand the geographic range of the genus and strongly suggests a Tethyan distribution for the genus. It also extends the genus into the Eocene, crossing the Cretaceous/Paleogene boundary. *Raninoides* is a new occurrence in the Bateque Formation but was already well known from both the North Pacific and Central American Eocene. *Paracorallicarcinus* occurs in the Eocene in Italy; there is insufficient age resolution at this time to determine which species is older, but the distribution pattern appears to have been Tethyan. Thus, Tethyan and North Pacific distribution patterns seem to have been dominant for the Bateque fauna at this time.

Paleoecology: The decapods recovered from the Bateque Formation are typical of a variety of environments. For example, *Calappilia* is typical of carbonate, subtropical to tropical habitats with a general Tethyan distribution as is *Lobonotus* (Schweitzer *et al*., 2002; Schweitzer *et al*., 2004b) and *Archaeotetra*, a member of the Trapeziidae (Schweitzer, 2005). Members of *Raninoides* have a very broad distribution geographically (Table 2) and in terms of depth of occurrence (Tucker, 1995), suggesting that the genus is eurytopic and quite adaptable, which is also suggested by its very long geologic range. *Prehepatus* is known primarily from intercontinental or shallow shelf deposits (references herein). However, members of the Homolidae generally occur in cooler water or deeper habitats as do members of the Cancridae (Schweitzer and Feldmann, 2000b; Schweitzer *et al*., 2004a); thus, the occurrence of all of these taxa within the same unit is unusual. In addition, most of the occurrences of the Cancrinae, the subfamily to which *Anatolikos* belongs, are in the temperate to high southern or northern latitudes (Schweitzer and Feldmann, 2000b), making the occurrence of the genus in Baja California even more aberrant.

We suggest that the occurrence of cool and warm and shallow, intermediate, and deep water taxa may be a result of several major factors. One is the position of Baja California at the crossroads of two major distributional pathways for decapods, the North Pacific and the Tethyan (Schweitzer, 2001b), which would have resulted in mixing of genera typical of both regimes. Another is the fact that the Bateque Formation appears to be comprised of sediments deposited in an offshore setting, probably the result of downslope mixing on an active plate margin with a short continental shelf, typical of other settings in which decapods are found on the west

coast of North America (Feldmann *et al*., 1991). Schweitzer (2001b) has already noted that the Eocene decapod faunas of the Pacific Slope of North America were quite diverse, probably as a result of the warmer climate of the time, and that Tethyan and subtropical genera were present in Eocene deposits of the Pacific Northwest of North America even further north than Baja California Sur. The composition of the fauna of the Bateque Formation supports her suppositions.

The Bateque and Tepetate formations have been considered to be very similar to one another on past occasions, even being considered to be the same formation (Hausback, 1984; Squires and Demetrion, 1992; 1994). A comparison of the decapod fauna from the two units suggests that while they may be similar in terms of age and some aspects of the other faunal elements, there were clearly environmental differences between the two units. To date, twenty-seven decapod taxa have been described from the Bateque Formation, and eight from the Tepetate Formation. Of these, only four of the taxa are shared between the two formations, including *Paguristes mexicanus* (Vega *et al*., 2001); *Lophoranina bishopi* Squires and Demetrion, 1992; *Calappilia hondoensis*; and *Lobonotus mexicanus*. Ongoing work by the authors has the possibility of yielding a small number of new taxa from the Tepetate Formation, but not nearly enough to close the large gap between the number of decapods in the two formations. In addition, preliminary analysis does not suggest that there will be a marked increase in overlap between the two faunas.

The paleoenvironmental conditions in the Bateque Formation were thus apparently much more conducive to either decapod diversity and/or their preservation. The latter seems unlikely to be the biasing agent, as the decapods are actually much better preserved in the Tepetate Formation, retaining more cuticle, appendages, and the ventral aspects of the carapace in many cases.

Acknowledgements

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